Transactions of the American Fisheries Society 134:1213–1227, 2005

DOI: 10.1577/T04-116.1

[Article]

Migration Depths of Adult Spring and Summer Chinook Salmon in the Lower Columbia and Snake Rivers in Relation to Dissolved Gas Supersaturation

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Abstract.—High spill volume at dams can create supersaturated dissolved gas conditions that may have negative effects on fish. Water spilling over Columbia and Snake River dams during the spring and summer creates plumes with high dissolved gas that extend downstream of dam spillways and throughout reservoirs and creates gas-supersaturated conditions throughout the water column. During the spring and summer of 2000, 228 adult Chinook salmon *Oncorhynchus tshawytscha* were tagged at Bonneville Dam with archival radio data storage transmitters (RDSTs) that recorded depth and water temperature as the fish migrated through dams and reservoirs of the lower Columbia and Snake rivers. Swimming depths from 131 of the 228 adult spring and summer Chinook salmon tagged with RDSTs were used to estimate the potential for gas bubble formation given in-river dissolved gas concentrations and hydrostatic compensation. We found that adult spring and summer Chinook salmon spent a majority of the time at depths that would have provided adequate hydrostatic compensation for in-river dissolved gas conditions during this study, which were at or slightly below long-term averages. Adult spring and summer Chinook salmon spent a majority of their time at depths deeper than 2 m, interspersed with periods lasting minutes at depths shallower than 2 m. Statistical associations were weak between the percent and duration of time fish occupied depths near the surface and dissolved gas concentrations, suggesting a lack of behavioral avoidance. Collectively, these data suggest little potential for negative effects of gas supersaturation on adult spring and summer Chinook salmon under average river conditions, despite the fact that fish tissues were probably supersaturated with dissolved gases. However, additional research over a broader range of dissolved gas conditions is needed to confirm that short, but frequent, exposure to conditions conducive to gas bubble formation does not affect survival and reproductive potential.

Gas bubble disease (GBD) is a condition that can affect fish and aquatic invertebrates residing in water that has become supersaturated with atmospheric gases as a result of either natural phenomena (e.g., photosynthesis, waterfalls) or human activity (hydroelectric projects). Within the Columbia River basin supersaturated conditions routinely occur in the lower Columbia and Snake rivers during the spring and summer and are largely attributed to the entrainment of atmospheric air as water is spilled at dams. While the spilling of water at dams has been one management strategy used to increase the survival of Columbia River basin juvenile salmonids *Oncorhynchus* spp. (Schoeneman et al. 1961; Muir et al. 2001), the voluntary use of spill poses a potential conflict with the management of adult salmonids because the spill period coincides with the timing of the upstream migration of adult spring and summer Chinook salmon *O. tshawytscha* and steelhead *O. mykiss*. Supersaturated conditions persist throughout the length of the lower Columbia and Snake rivers as well as the water column because the lack of strong turbulence does not allow water to equilibrate with the atmosphere (Ebel 1969). Exposure to supersaturated water in adult fishes is most likely to occur in reservoirs and tailraces, and near

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Received February 25, 2005; accepted March 31, 2005
Published online August 10, 2005

fishway entrances at dams; it is less likely to occur inside fishways because adult fish ladders quickly degas supersaturated water (Bouck 1996).

Supersaturated water conditions can cause GBD or gas bubble trauma (GBT) in fish through the formation of excessive bubbles in tissues and body fluids which then cause potentially lethal vascular and cardiac blockage or hemorrhaging. Bubbles form when the tissues and fluids of fish become saturated or supersaturated after exposure to supersaturated water conditions and the pressures of dissolved gases in fish tissues exceed the sum of barometric and hydrostatic pressures (Weitkamp and Katz 1980; Colt 1984), a process that is analogous to ''the bends'' in human divers. Therefore, fish depth plays a central role in the expression of GBD and GBT because the hydrostatic pressure has a strong influence on the total dissolved gas supersaturation (TDGS) exposure to individual fish. Each meter of depth exerts pressure that increases the solubility of dissolved gas to compensate for approximately 10% of saturation, where 100% represents fully saturated water (Weitkamp and Katz 1980). Consequently, an increase in fish depth provides a rapid and linear decrease in the potential for GBD. Conversely, a reduction in the depth by fish with saturated or supersaturated tissues increases the risk of bubble formation as the hydrostatic pressure drops. In addition to direct effects, GBT has also been known to increase a fish's susceptibility to disease and predation, and reduced growth and swimming performance (Dawley and Ebel 1975). Maintaining a single depth where adequate hydrostatic compensation is achieved may not be required to avoid GBD. Intermittent periods of hydrostatic compensation through changes in depth of swimming reduced signs of gas bubble disease (Meekin and Turner 1974; Dawley et al. 1975; Weitkamp 1976; Knittel et al. 1980).

The level of in-river dissolved gas supersaturation that salmonids can safely tolerate varies depending on species, body size, duration of exposure, general physical condition, swimming depth, and water temperature (which affects the solubility of dissolved gasses; Ebel et al. 1975; Weitkamp and Katz 1980). Wood (1968) identified nitrogen saturation of 118% to be detrimental to adult salmonids. Rucker and Tuttle (1948) indicated gas supersaturation between 110% and 115% as the critical range for gas bubble formation in adult salmonids. Westgard (1964) found that adult Chinook salmon held in water at a nitrogen saturation of 116% developed symptoms of GBD. In 1968, supersaturated levels from 123% to 143% (related to construction of John Day Dam) resulted in substantial juvenile and adult salmon and steelhead mortalities and signs of GBD (Beiningen and Ebel 1970). Gas levels in the lower Columbia River during spring migration are typically below 120–125%, but frequently exceed 130–135% under high discharge conditions (U.S. Army Corps of Engineers 1998).

Fish may be able to avoid areas of higher dissolved gas concentrations by moving laterally if spatial heterogeneity in dissolved gas concentrations exist (such as in a dam tailrace) or by sounding to depths where hydrostatic pressure is sufficient to compensate for supersaturation. Hydrostatic compensation or lateral movement away from higher dissolved gas concentrations was observed with adult summer and fall Chinook salmon in the lower Snake River using depth-sensitive tags (Gray and Haynes 1977), suggesting fish can detect and avoid supersaturated water. Avoidance of gas-supersaturated water was also observed in laboratory experiments with juvenile Chinook salmon (Meekin and Turner 1974; Dawley et al. 1975), juvenile rainbow trout *O. mykiss*, coho salmon *O. kisutch*, sockeye salmon *O. nerka*, and Chinook salmon (Stevens et al. 1980). However, studies with juvenile steelhead (Blahm et al. 1975; Dawley et al. 1975; Stevens et al. 1980), rainbow trout (Lund and Heggberget 1985), and juvenile Chinook salmon (Ebel 1971) showed no indication of avoidance of gas-supersaturated water. Other studies indicate avoidance of only extreme levels of gas supersaturation. Common carp *Cyprinus carpio* and black bullhead *Ameiurus melas* responded only to dissolved gas levels exceeding 145% (Gray et al. 1983). Similarly, juvenile coho salmon, sockeye salmon, Chinook salmon, and rainbow trout avoided levels that exceeded 125%, but not always 115% (Stevens et al. 1980).

Few studies have examined how gas supersaturation affects the upstream migration of anadromous fishes in large river systems that have been altered by hydroelectric development. Our study objectives were to (1) evaluate the migration depth of adult spring and summer Chinook salmon in a riverine environment where gas-supersaturated conditions exist to estimate the potential for GBD expression in migrating adults, and (2) evaluate associations between the migration depth of adults and the total dissolved gas concentration of the water in the lower Columbia and Snake rivers as a preliminary test of whether fish altered their mi-

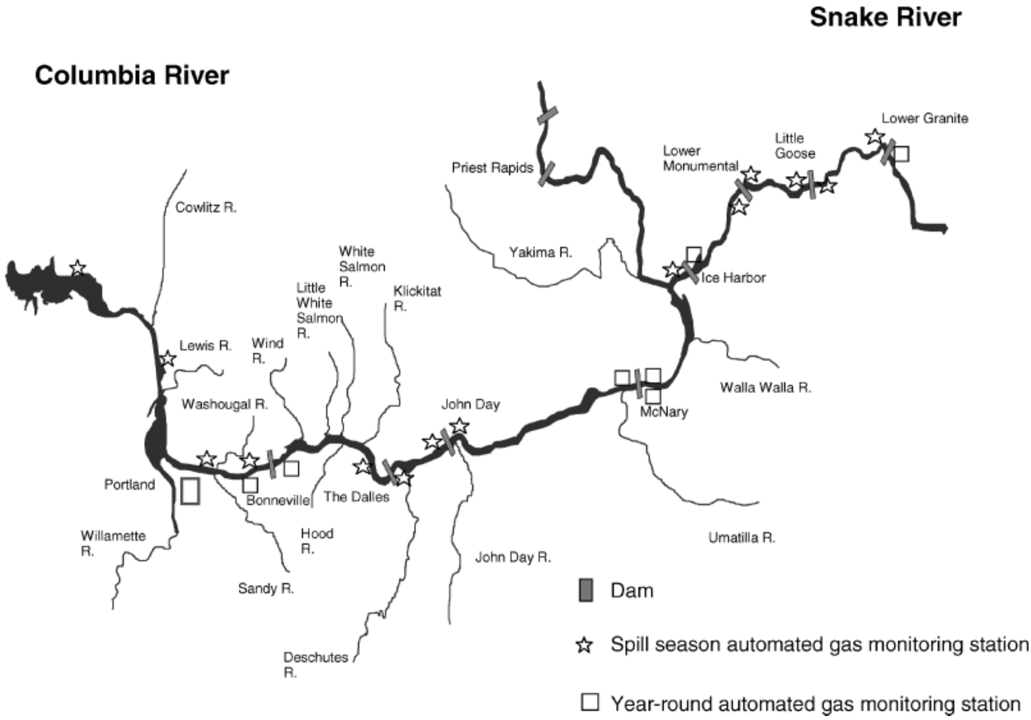

FIGURE 1.—Map of the Columbia and Snake rivers, where the migration of radio-tagged adult spring and summer Chinook salmon was monitored during 2000. The locations of major tributaries, dams, and gas monitoring stations are also shown.

gration behavior when encountering supersaturated conditions.

Methods

Study area.—Our study area included the lower Columbia River from release sites at river kilometer (rkm) 225.9 (located approximately 9 km below Bonneville Dam) upstream to the confluence of the Columbia and Snake rivers (rkm 521.6), and the lower Snake River from the mouth upstream to Lower Granite Dam (rkm 694.6; Figure 1; river kilometers are measured from the mouth of the Columbia River).

Tagging procedures.—Adult Chinook salmon were trapped and tagged from 4 April through 31 July 2000 at the adult fish facility located adjacent to the Washington shore fishway at Bonneville Dam. A total of 228 adult spring and summer Chinook salmon were tagged intragastrically with a 3-V (9 × 2 cm; 34 g in air) radio data storage transmitter (RDST). Radio data storage transmitters were programmed to record temperature at 1-min intervals and pressure at 5-s intervals during upstream migration, which allowed 40 d of data storage. Accuracy of the pressure sensor in the RDST was 4.8 kPa (0.5 m), and the accuracy of the temperature sensor was 0.15°C at water temperatures of 0–20°C. These transmitters were placed in spring and summer Chinook salmon thought to be of Snake River origin based on passive integrated transponder (PIT) tag codes and adipose fin clips so that tags could be recovered at Lower Granite Dam (Figure 1). Fish that reached Lower Granite Dam were diverted from the fish ladder into the adult fish trap based on select PIT or coded wire tags. Most (97%) fish tagged with a RDST were of hatchery origin. More details on tagging methods and the adult fish facility can be found in Keefer et al. (2004a).

Chinook salmon movements past dams, through reservoirs, and into tributaries were determined by means of fixed radio receivers (radio receivers connected to aerial antennas or underwater antennas) located at all major tributaries and dams in the Columbia and lower Snake rivers. Aerial antennas were used with sequentially scanning receivers (6 s per frequency), while underwater antennas were used in combination with SRX–DSP receivers capable of simultaneously monitoring several radio transmitter frequencies and antennas.

The migration history of individual fish was separated into passage segments in reservoirs and in the tailrace of dams. Fish were considered to be in the tailrace of a dam based on the time period between the last record on the directional aerial antennas located downstream of each dam (range, 0.5–3.2 km) and entry into a fishway at the dam based on records from underwater antennas located at the fishway entrances, the collection channel, and at the navigation lock. Times spent in reservoirs were determined from the last record at the top of the fish ladder at a downstream dam and the first record at the tailrace antenna at the upstream dam. Times spent in monitored tributaries were excluded from this analysis. The Wind, Little White Salmon, White Salmon, Klickitat, Hood, Deschutes, and John Day rivers were continually monitored by fixed receivers and antennas (Figure 1). In addition, Eagle Creek and Herman Creek were monitored on a weekly basis from boat or truck. Data processing involved assigning codes to identify a fish's movement within and around a dam or tributary. A more complete explanation of data collection and processing procedures can be found in Keefer et al. (2004b).

We examined patterns of depth use throughout the migration by calculating the median migration depth of each fish in each Columbia and Snake River reservoir or tailrace using the RDST data. Medians are reported and used in statistical analyses rather than means because depth distributions were asymmetrical and skewed towards deeper depths. Mixed-model, repeated-measures analysis of variance (ANOVA) was used to test for differences in the median migration depth of individual fish (= subjects) among reservoir or tailrace locations (fixed effect), and using compound symmetry as the covariance structure. The Kenward–Roger method estimated degrees of freedom, resulting in fractional degrees of freedom. Multiple comparisons of the median migration depth for groups of individuals at each reservoir or tailrace were performed using a Tukey-type post hoc statistic (Zar 1999).

Degree of exposure to TDGS was estimated as the percentage of time fish were observed near the surface (between 0 and 2 m), and the duration of depth-uncompensated exposure was determined as the successive depth records shallower than 1 and 2 m. The limited coverage of dissolved gas monitoring stations in the system made it difficult to determine the levels of dissolved gas encountered by the fish. Therefore, we evaluated the depth of migration that would provide a reduction of 10% and 20% total dissolved gas pressure (TDGP) through hydrostatic compensation because this degree of compensation should have prevented tissue bubble formation despite exposure to supersaturated conditions given the degree of supersaturation observed in-river (Figure 2).

Linear regression analysis was used to evaluate relationships between water supersaturation and migration depth during passage through reservoirs and tailraces. The independent variable used in this regression model was the average total dissolved gas percentage weighted by the duration of time an individual fish was observed in a reservoir or tailrace. Total dissolved gas concentrations were measured hourly at a depth of 2–3 m by a fixed monitoring station located in the forebay of the reservoir and tailrace of each dam on the Columbia and Snake rivers. The percentage of time individual adult spring and summer Chinook salmon were observed deeper than 1 and 2 m, and the continuous amount of time shallower than 1 and 2 m at each dam, were dependent variables in the linear regression models. Time spent deeper than 1 and 2 m was arcsine transformed, and time spent shallower than 1 and 2 m was $\log_e$ transformed to improve homogeneity of the variances and normality of the residuals (Zar 1999).

Results

Of the 228 adult spring and summer Chinook salmon tagged with RDSTs in 2000, 137 tags were recovered (60% recovery rate) and 131 were used to evaluate the depth of migration. Six RDSTs were unusable due to a malfunctioning pressure sensor or improper tag setup. The majority of the fish tagged with RDSTs (53%) were recaptured at the Lower Granite Dam adult fish trap and provided an extensive history of each fish's migration depth through the lower Columbia and Snake rivers. Hatcheries (21%), tribal and sport fishery (16%), and spawning grounds and weirs (10%) accounted for the remaining RDSTs returned. Based on the last telemetry records of fish at fixed receiver sites, 58% of the unaccounted RDSTs were last detected upstream of Priest Rapids Dam, 31% in the lower Columbia River downstream of John Day Dam, and 11% in the Columbia River between Priest Rapids and John Day dams.

The median depth of most individuals migrating through lower Columbia and Snake River reservoirs and dam tailraces was greater than 2–3 m (Figures 3, 4). Median migration depths of adult spring and summer Chinook salmon were significantly deeper at Bonneville and the Dalles res-

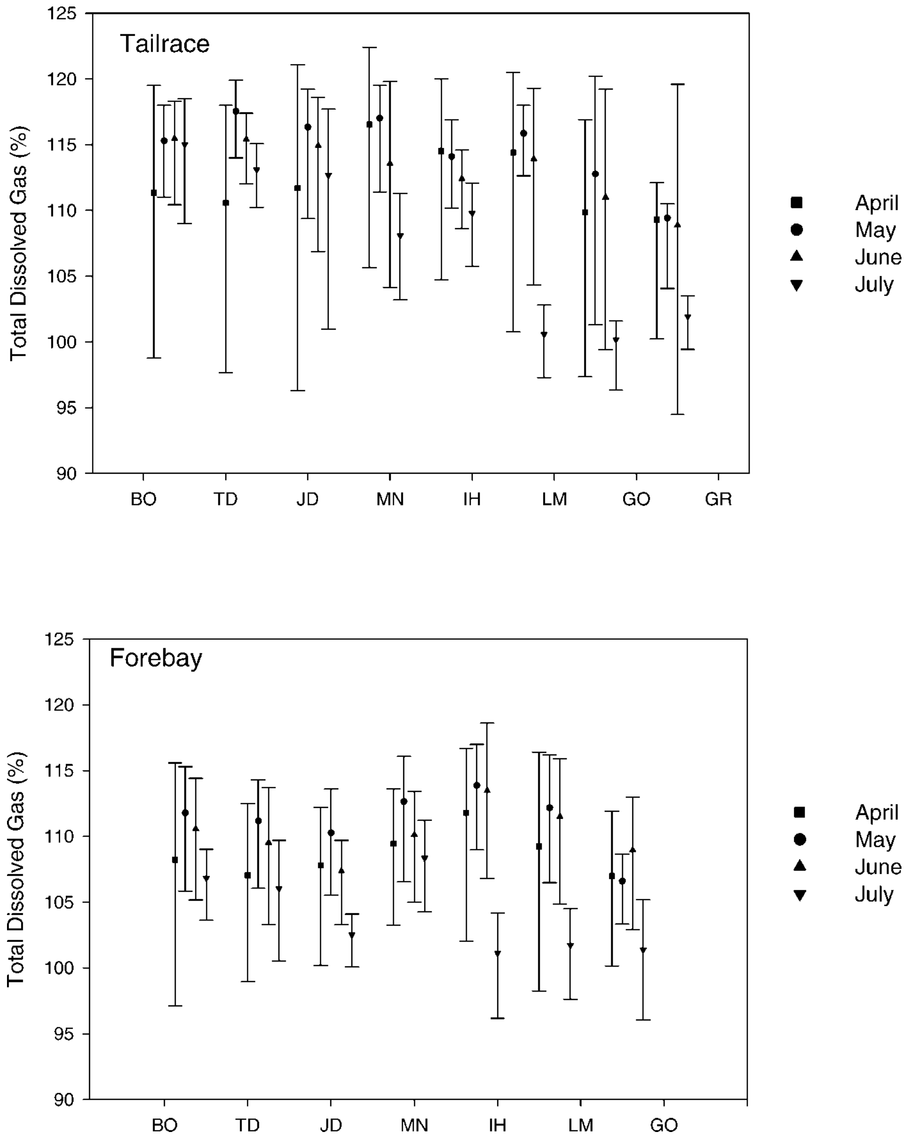

FIGURE 2.—Mean and 90th percentiles of hourly total dissolved gas concentrations in the lower Columbia and Snake River dam tailraces and forebays, April–July 2000. Abbreviations are as follows: BO = Bonneville Dam, TD = the Dalles Dam, MN = McNary Dam, IH = Ice Harbor Dam, LM = Lower Monumental Dam, GO = Little Goose Dam, GR = Lower Granite Dam. Data are from the U.S. Army Corps of Engineers, 1998.

ervoirs than at upstream reservoirs (repeated-measures ANOVA: df = 6, 87.7; $F = 39.4$; $P < 0.0001$; Figure 3). Similarly, median depths in tailraces were greater at lower Columbia River dams than at Snake River dams (repeated-measures ANOVA: df = 7, 107; $F = 40.0$; $P < 0.0001$; Figure 4). Median migration depths were the shallowest in the Ice Harbor tailrace (Figure 4). Interestingly, there was a significant effect of subject (= fish) in the repeated-measures test, indicating the relative depth use of individual fish was consistent among reservoirs (i.e., some fish consistently used relatively deep water while others used relatively shallow water).

Adult spring and summer Chinook salmon swam at depths greater than 2 m a majority of the time when migrating through reservoirs in the lower Columbia and Snake rivers. The percentage of time fish were at least 2 m below the surface (providing at least 20% hydrostatic pressure compensation)

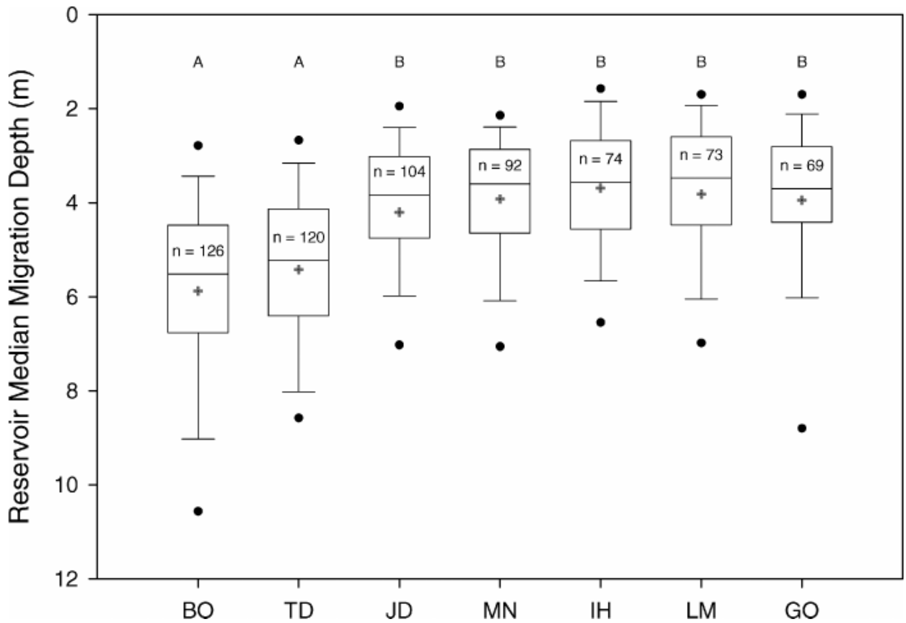

FIGURE 3.—Means (crosses within boxes), medians (horizontal lines within boxes), quartiles (upper and lower bounds of boxes), 10th and 90th percentiles (ends of whiskers), and 5th and 95th percentiles (circles) of migration depths for adult spring and summer Chinook salmon during migration through the four lower Columbia River and three lower Snake River reservoirs in 2000. Abbreviations are as follows: BO = Bonneville, TD = the Dalles, JD = John Day, MN = McNary, IH = Ice Harbor, LM = Lower Monumental, and GO = Little Goose. Medians that are significantly different are indicated by different letters (Tukey's post hoc test; $P \leq 0.05$).

during migration through a reservoir ranged from 66% at Ice Harbor to 85.1% at Bonneville (Figure 5). Fish were deeper than 1 m (providing at least 10% hydrostatic pressure compensation) ranging from 90.7% of the time in the Little Goose Reservoir to 97% of the time in the Bonneville Reservoir (Figure 5). The relationship between the dissolved gas saturation of the water and the percentage of time fish were deeper than 2 m in the water column was significant though weak for Bonneville Reservoir (linear regression: df = 124; $P < 0.001$; $r^2 = 0.177$) and the Dalles Reservoir (df = 116; $P < 0.001$; $r^2 = 0.117$).

Adult spring and summer Chinook salmon generally migrated deeper in tailraces than in reservoirs. The percentage of time spent at least 2 m below the surface during migration through a tailrace ranged from 86.4% at Ice Harbor to 93.7% at Bonneville (Figure 5). The percentage of time deeper than 1 m ranged from 97.7% in the Little Goose tailrace to 99.6% in the Dalles tailrace (Figure 5). These depths also imply near continuous hydrostatic compensation.

Adult spring and summer Chinook salmon frequently altered their depth in the water column (Figure 6). The duration of time adult Chinook salmon typically occupied surface waters ranged from minutes at a time at depths less than 2 m to seconds at depths less than 1 m (Figure 7, 8). The maximum successive time less than 1 m and less than 2 m observed by an individual fish outfitted with an RDST during migration through a reservoir was 1.3 and 19.5 h, respectively. Although durations of time near the surface were short, we found that adult spring and summer Chinook salmon frequently reascended to surface waters. The median duration of time spent more than 2 m deep in the water column before reascending to a depth above 2 m ranged from 2.1 min in the Ice Harbor Reservoir to 3.4 min in the Dalles Reservoir (Figure 7). The median duration of time spent more than 1 m deep in the water column before reascending to a depth above 1 m ranged from 6.6 min in the Little Goose Reservoir to 33.5 min in the Bonneville Reservoir (Figure 8).

Regressions of swimming depth versus supersaturated gas exposure revealed significant but weak increases in depth with increasing TDG at some locations but not others. Significant but weak positive relationships ($r^2 = 0.059–0.108$; $P \leq 0.013$) were observed between the total dissolved gas saturation of the water and the percentage of

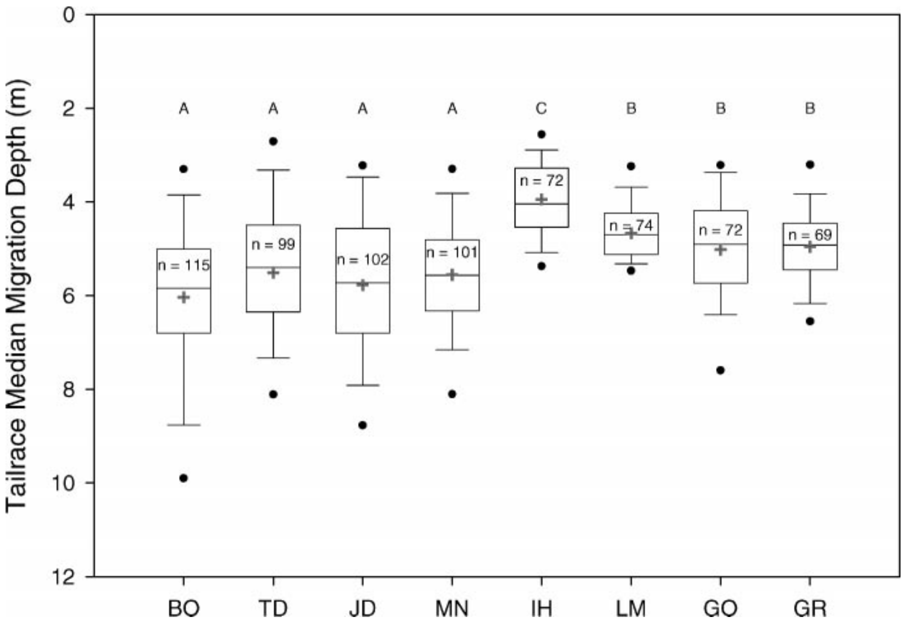

FIGURE 4.—Means (crosses within boxes), medians (horizontal lines within boxes), quartiles (upper and lower bounds of boxes), 10th and 90th percentiles (ends of whiskers), and 5th and 95th percentiles (circles) of median migration depths for adult spring and summer Chinook salmon in the tailrace sections of the four lower Columbia River dams and four lower Snake River dams in 2000. Abbreviations are as follows: BO = Bonneville, TD = the Dalles, JD = John Day, MN = McNary, IH = Ice Harbor, LM = Lower Monumental, GO = Little Goose, and GR = Lower Granite. Medians that are significantly different are indicated by different letters (Tukey's post hoc test; $P \leq 0.05$).

time fish were deeper than 1 m in Columbia River reservoirs but not lower Snake River reservoirs ($P \geq 0.25$). The relationships between dissolved gas saturations and the percentage of time fish were deeper than 2 m in the water column was significantly positive ($P \leq 0.04$) but weak in all but the Bonneville tailrace as r^2 values ranged between 0.062 at Lower Granite to 0.196 at McNary. Significant positive relationships existed between the total dissolved gas saturation and the percentage of time deeper than 1 m in the John Day tailrace (linear regression: df = 99; $F = 5.47$; $P = 0.021$; $r^2 = 0.05$) and McNary tailrace (df = 99; $F = 4.24$; $P = 0.042$; $r^2 = 0.04$). No significant relationships were observed between dissolved gas levels and the average continuous time fish spent shallower than 2 m in the water column during migration through a reservoir. Significant but weak negative relations existed between the average continuous time below 1 m in the water column and the dissolved gas saturation of the water in the Bonneville Reservoir (linear regression: df = 122; $F = 7.5$; $P = 0.007$; $r^2 = 0.058$) and John Day Reservoir (df = 101; $F = 8.4$; $P = 0.005$; $r^2 = 0.077$).

Discussion

We found that adult spring and summer Chinook salmon migrating through reservoirs and tailraces in the lower Columbia and Snake rivers spent a majority of the time at depths that should have provided adequate hydrostatic compensation for supersaturated river conditions in the range of 120% or more. The observed depth use of adult spring and summer Chinook salmon may explain the relatively low incidence of GBD in adult Chinook salmon sampled at Bonneville Dam when gas supersaturation levels are lower than 120–125% (Backman and Evans 2002). Our results on depth use between the surface and 2 m are consistent with those of Gray and Haynes (1977) who found that adult spring Chinook salmon spent approximately 89% of their time at least 2 m below the surface in the Snake River downstream of Little Goose Dam when gas saturation levels were below 130%. We observed that tagged fish swam deeper than 2 m in the tailrace of Little Goose Dam about 87% of the time under similar saturation levels. The highest percentage of time recorded near the surface was in the lower Snake River downstream

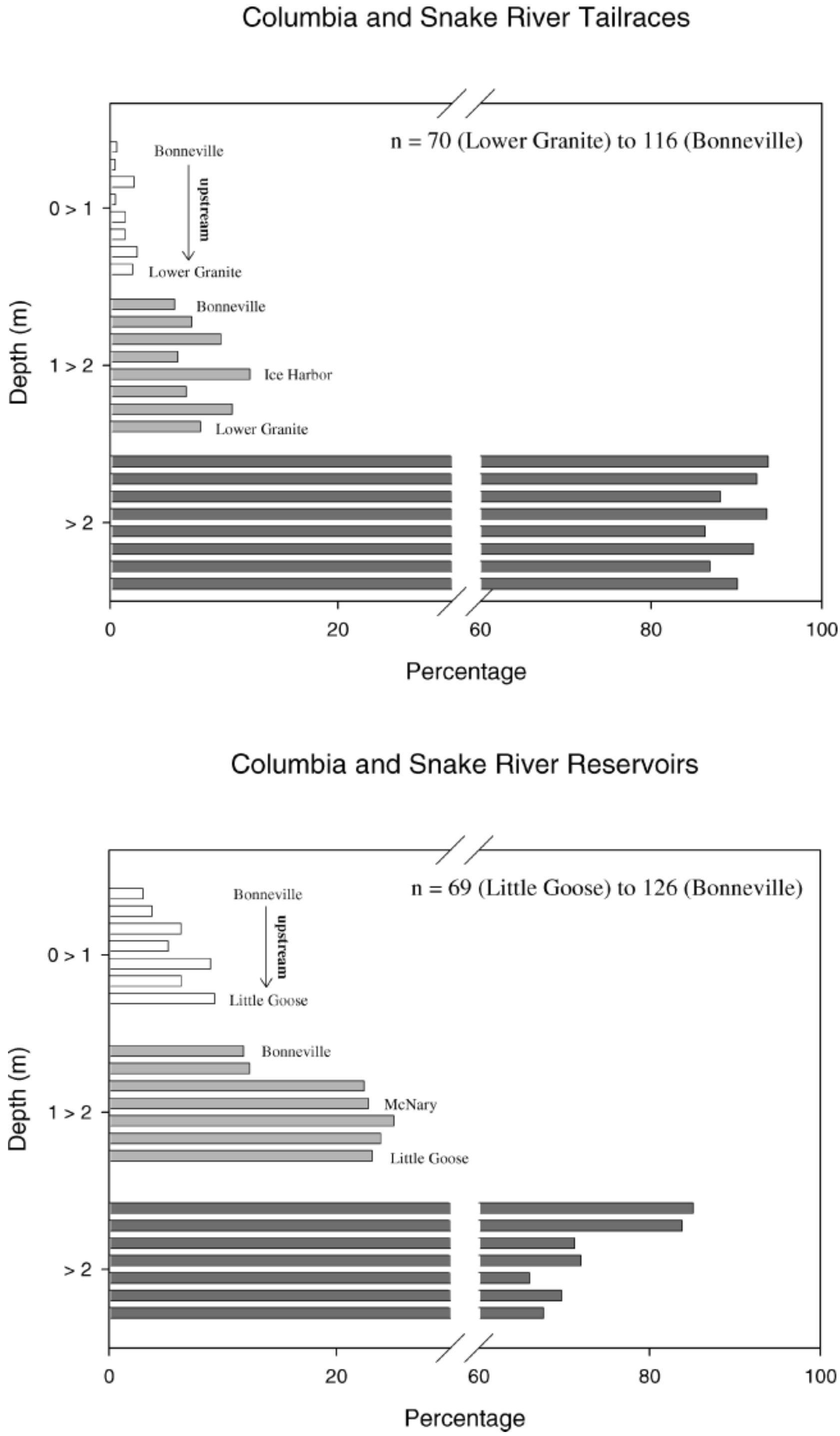

FIGURE 5.—Percentage of time spent between the surface and 2 m by adult spring and summer Chinook salmon tagged with radio data storage tags (RDSTs) during migration through tailraces (top panel) and reservoirs (bottom panel) of the Columbia and Snake rivers. Bars represent the percentage of time (pooled for all fish) spent at a given depth in each reservoir and dam tailrace.

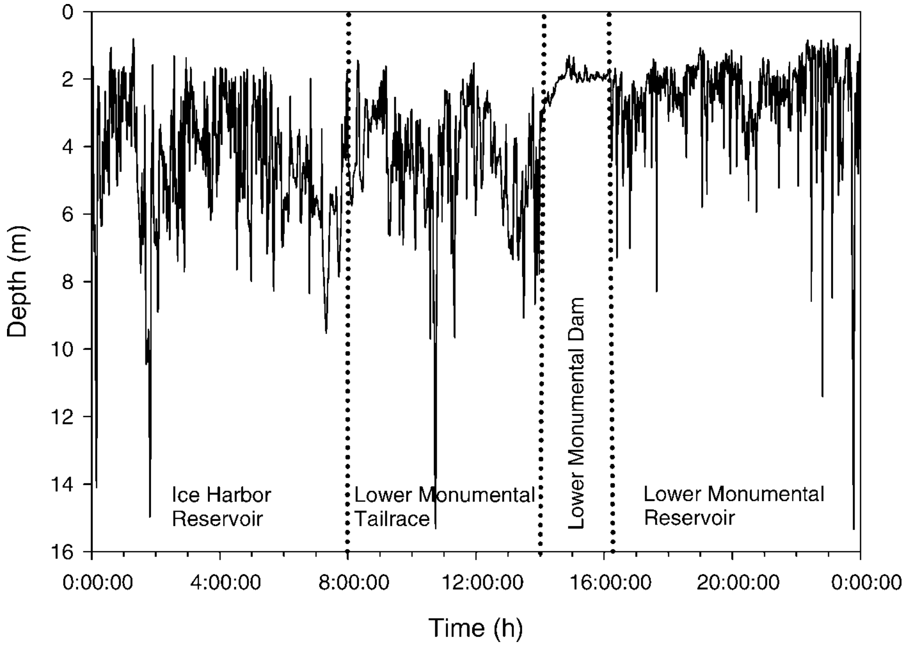

FIGURE 6.—The swimming depth at 1-min intervals of an adult Chinook salmon (RDST 2480B) on 3 June 2000 in the lower Snake River.

of Ice Harbor Dam and is likely a result of available depth. Water depth in the Ice Harbor tailrace is shallow compared with that of other tailraces, typically less than 2–3 m along the south shoreline or greater than 10 m deep along the north shore, where the shipping channel is located. Shrank et al. (1997) observed that GBD was prevalent in fish downstream of Ice Harbor Dam under highly supersaturated conditions (>130% TDGS) but was rare in other reaches of the Columbia and Snake rivers.

We found that adult spring and summer Chinook salmon tended to migrate deeper in tailraces than in reservoirs. Adult salmon tend to migrate in close proximity to shorelines (Reischel and Bjornn 2003; Hughes 2004), and the steep gradient shorelines common in the dam tailrace compared with those in reservoirs may have increased tailrace swimming depths. Alternatively, differences in water velocity, temperature, or dissolved gas levels between tailrace and reservoir reaches of the river may have been responsible.

The combination of the extent of TDGS and the frequency and duration of descents deeper than compensation depth largely determines the development and severity of GBD (Weitkamp and Katz 1980; Elston et al. 1997; Hans et al. 1999; Weitkamp et al. 2003). Results from past studies indicate that GBD symptoms become more detrimental as duration of exposure increases (Weitkamp and Katz 1980). Based on reservoir passage times of up to several days, adult Chinook salmon are exposed to gas supersaturation for long periods (Keefer et al. 2004b). However, although adult spring and summer Chinook salmon frequently entered the upper 2 m of the water column, excursions to shallow depths were brief, ranging from seconds for depths less than 1 m to minutes for depths less than 2 m. Effects of short but frequent depth-uncompensated exposure patterns that we observed in adult spring and summer Chinook salmon on the prevalence of GBD and mortality are not well understood. Previous studies have shown that intermittent deep and shallow water exposure produced fewer signs of GBD and mortality than what is the case for those fish unable to change depth (Dawley et al. 1975; Weitkamp 1976; Knittel et al. 1980). Due to the number of variables involved, the time required for the formation of emboli that would result in the physical appearance of GBD and mortality can vary considerably. The appearance of GBD involves bubble formation and bubble growth to a size that blocks vascular flow. These times can vary as a result of interindividual susceptibility to GBD, location of emboli formation, fish depth, duration of compen-

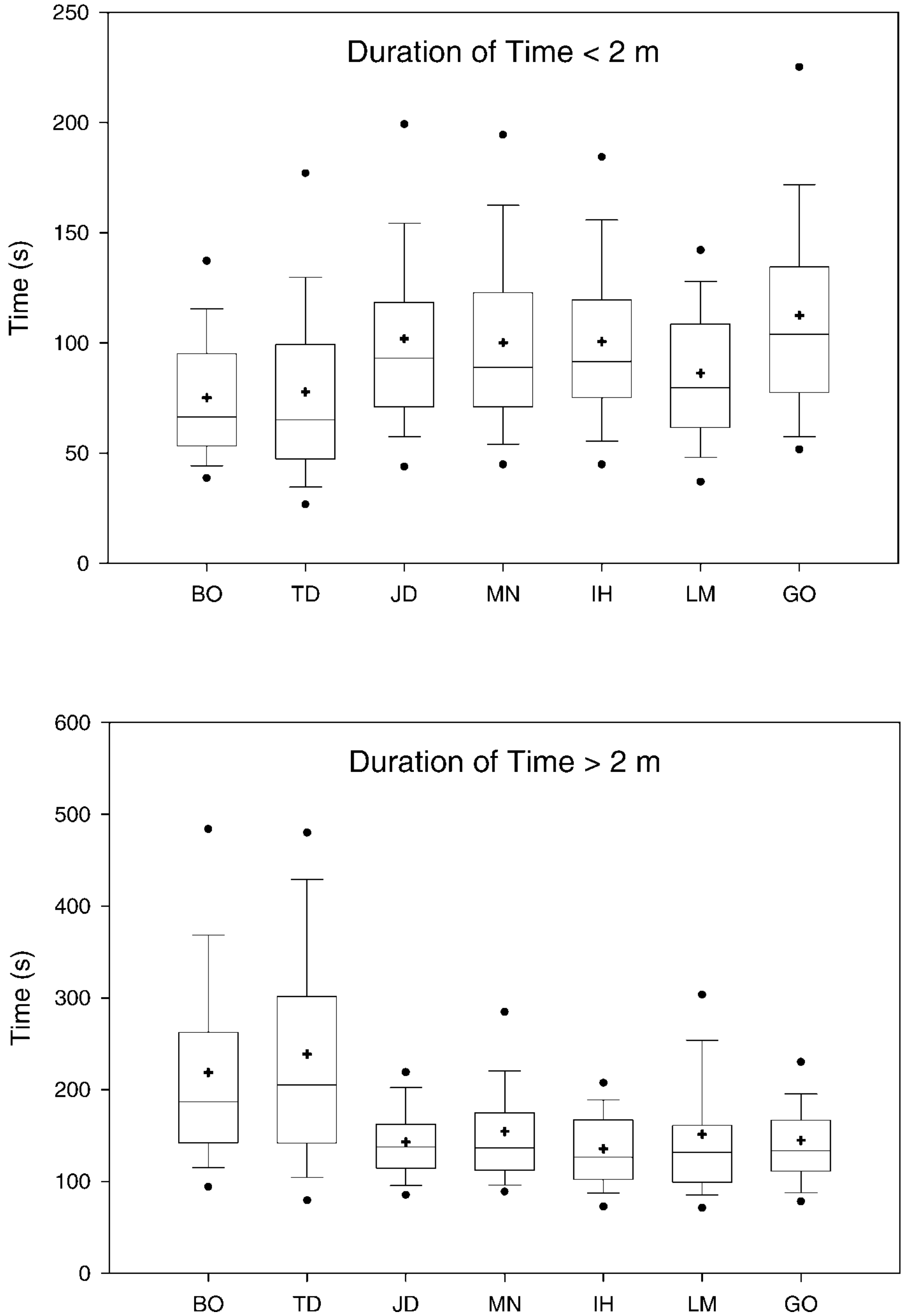

FIGURE 7.—Means (crosses within boxes), medians (horizontal lines within boxes), quartiles (upper and lower bounds of boxes), 10th and 90th percentiles (ends of whiskers), and 5th and 95th percentiles (circles) for consecutive time(s) (min) less than 2 m (top panel) and greater than 2 m (bottom panel) by adult spring and summer Chinook salmon during migration through the four lower Columbia River and three lower Snake River reservoirs. Abbreviations are as follows: BO = Bonneville (n = 126), TD = the Dalles (n = 120), JD = John Day (n = 104), MN = McNary (n = 92), IH = Ice Harbor (n = 74), LM = Lower Monumental (n = 73), and GO = Little Goose (n = 69). Note that the scale of the y-axis differs between panels.

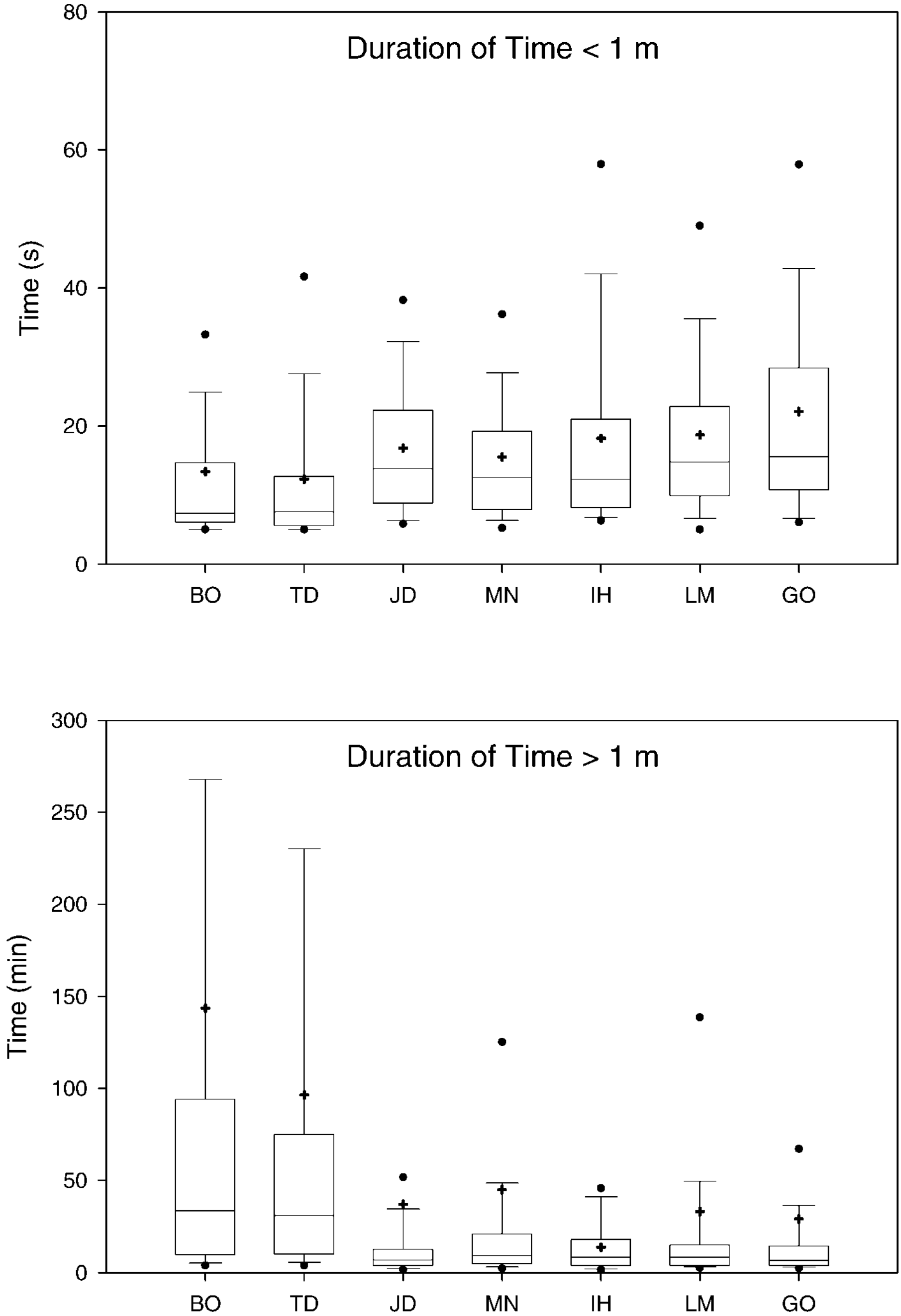

FIGURE 8.—Means (crosses within boxes), medians (horizontal lines within boxes), quartiles (upper and lower bounds of boxes), 10th and 90th percentiles (ends of whiskers), and 5th and 95th percentiles (circles) for consecutive time(s) (min) less than 1 m (top panel) and greater than 1 m (bottom panel) by adult spring and summer Chinook salmon during migration through the four lower Columbia River and three lower Snake River reservoirs. Abbreviations are as follows: BO = Bonneville (n = 126), TD = the Dalles (n = 120), JD = John Day (n = 104), MN = McNary (n = 92), IH = Ice Harbor (n = 74), LM = Lower Monumental (n = 73), and GO = Little Goose (n = 69). Note that the scale of the y-axis differs between panels.

satory depths in addition to other modifying influences (e.g., presence of residual bubbles, activity of the fish, and water temperature; Weitkamp and Katz 1980; Hans et al. 1999; Mesa et al. 2000; Morris et al. 2003). Available literature suggests significant bubble formation requires periods of tens of minutes to hours of insufficient hydrostatic pressure compensation and fish with supersaturated tissues would unlikely experience signs of gas bubble disease given the time scales of shallow-water use we observed. Morris et al. (2003) observed bubbles in the lateral line of juvenile Chinook salmon after the first hour of exposure at 125% and 130% TDGS. Mesa et al. (2000) observed complete occlusion of the lateral line after 2 h exposure at 130% TDGS, and 50% occlusion after 14-d exposure at 110% TDGS. Continuous vertical movements were observed in juvenile steelhead in a deep (10-m) aquarium, and no mortality was observed within 7 d at total dissolved gas levels of 130% (Dawley et al. 1975).

Even the longest continuous time recorded by an adult spring and summer Chinook salmon at depths above 1 and 2 m (1.3 and 19.5 h, respectively) would probably be insufficient to affect reproductive success or cause severe GBD symptoms and mortality based on the gas levels observed during 2000. Continuous exposure to gas-supersaturated water—46 h at 114% TDGS and 10 h at 125% TDGS in 0.5-m-deep tanks—had no effect on the prespawning mortality or reproductive success of female Chinook salmon late in their maturation (Gale et al. 2004). Ebel et al. (1975) reported that 25-d continuous exposure was needed to cause substantial mortality in both juvenile and adult salmon confined to shallow water (1 m) at a saturation level of 115% TDGS. Nebeker (1973) indicated that the lethal time that resulted in death of 50% of the exposed population (LT50) for adult Chinook salmon at 125% TDGS in a shallow tank was approximately 17 h. For adult sockeye salmon, which tend to be less tolerant than Chinook salmon of TDG exposure, the time that resulted in death of 40% of the exposed population (LT40) was 127 h at 120% TDGS and 835 h at 115% TDGS (Nebeker et al. 1976). These fish were restrained to a maximum depth of 60 cm.

Frequent dives into the water column (below the hydrostatic compensation depth) may provide an opportunity to recover from exposure to supersaturation as a result of gas bubble reabsorption. For fish remaining below the compensation depth, gas bubbles will eventually be dissolved and transferred into the plasma or cellular fluids (Elston et al. 1997). The time it takes for bubble reabsorption can vary depending on GBD severity, location of bubbles, and the pressure differential (Elston et al. 1997; Hans et al. 1999). Rapid bubble reabsorption (5 min) was observed in yearling Chinook salmon exposed to a hydrostatic pressure equivalent to 30 m (Elston et al. 1997). Rapid recovery from the potentially lethal effect of supersaturation can also occur when moving from water with high supersaturation to water with near normal supersaturation (Hans et al. 1999). Lateral gradients of supersaturated water that exist downstream of dams and tributaries in the lower Columbia River may provide refuge from gas-supersaturated water (Scheibe and Richmond 2002). Although our results do not demonstrate that bubble reabsorption occurs in upriver migrants, the observed depth histories indicate that if bubble formation occurs during near surface excursions, bubble reabsorption is possible.

We found no strong relationships or trends between the dissolved gas concentration of the water and the proportion of time fish spent near the surface. Vertical avoidance responses to dissolved gas saturation may occur only at saturation levels higher than those typical of the Columbia and Snake rivers in 2000 (Gray et al. 1983; Gray and Haynes 1977; Stevens et al. 1980). While logistic constraints on our experimental design could have contributed to the lack of relationship observed between migration depth and dissolved gas concentrations, we believe the lack of a strong relationship resulted from fish behavior rather than sampling error for several reasons. Many lower Columbia River and Snake River dams increased spill volume during the nighttime to take advantage of the tendency of juvenile salmonids to pass dams at night (Brege et al. 1996), though these increases in spill generally resulted in small increases in TDGS levels (<5%) recorded by monitoring stations (U.S. Army Corps of Engineers 1998). We found that fish were generally deeper during the night (Figure 6); however, we did not observe strong evidence that behavior was different during periods of high, low, or no spill regardless of time of day. Individual fish did not appear to alter their behavior with respect to the duration or percent of time spent near the surface during varying supersaturated conditions. The short periods spent near the surface followed by return dives to deeper (>2-m) water could be interpreted as individual fish responding to the physiological effects of supersaturated tissues as they entered negative pressure conditions near the surface conducive to gas bubble formation. However, fall Chinook salmon tagged in a parallel study when average TDGS was 101% or less exhibited qualitatively identical patterns of frequent and rapid depth changes and very little (<5%) time spent at depths above 2 m (C. C. Caudill, unpublished data). The lack of changing behaviors of several species of salmonids in response to spill volume was also observed in the Clark Fork River (Weitkamp et al. 2003). Hence, while salmonids may be able to detect, and attempt to avoid, highly supersaturated conditions, we found no evidence that adult Chinook salmon strongly altered their behavior in the moderately supersaturated conditions during the study period.

Unaccounted-for RDSTs could have potentially biased our results because fish experiencing uncompensated exposure as a result of shallow migration would be less likely to successfully reach Lower Granite Dam or other destinations where the transmitter could be found and returned. However, based on last telemetry records at dams and tributaries, most unaccounted-for fish (58%) were detected last in the middle Columbia River upstream of Priest Rapids Dam (rkm 638.9). Radio transmitter return rates are substantially lower for the middle and upper Columbia River as a result of reduced coverage and tag recovery effort. Telemetry records indicate that 31% of the unaccounted-for fish were last detected in the lower Columbia River downstream of John Day Dam where transmitter regurgitation rates were highest (Keefer et al. 2004a). The remaining unaccounted-for RDSTs (11%) were last detected in the Columbia River between Priest Rapids and John Day dams. The general lack of evidence for the effects of GBD and the fact that most unaccounted-for fish migrated out of the lower Columbia River suggest that this source of error did not seriously bias our conclusions.

In conclusion, evaluation of adult spring and summer Chinook salmon migration depths indicates that the majority of the time was spent at depths that provided adequate hydrostatic compensation for supersaturated conditions in the range of 120% of saturation or more. We did not observe strong associations between migration depth near the surface and the dissolved gas concentration of the water. The significant but weak associations we found may be the result of a fish's inability to detect and avoid water conditions favoring bubble formation or the lack of highly supersaturated (i.e., >120% TDGS) conditions in-river. We caution that greater TDGS and behavioral responses may occur in years with higher discharge and spill conditions. Fish entered surface waters (<2 m) frequently, but the time spent there was usually brief. The apparent vertical movement into and out of the surface layer by adult spring and summer Chinook salmon suggests the need for additional research to identify the effects of frequent but short durations of depth-uncompensated exposure on the long-term survival and reproductive potential of the fish.

Acknowledgments

Many people assisted in the fieldwork and data compilation for this project. We thank J. Congleton and M. Keefer at the University of Idaho for reviewing this manuscript. M. Jepson, S. Clabough, University of Idaho; and A. Matter, National Marine Fisheries Service provided data management and technical support. This project was funded by the U.S. Army Corps of Engineers Walla Walla and Portland Districts. Reference to trade names does not imply endorsement by the U.S. Government.

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